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THE TYPE B SONG OF THE NORTHERN PARULA: STRUCTURE AND GEOGRAPHIC VARIATION ALONG PROPOSED SUB-SPECIES BOUNDARIES

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ABSTRACT.—The type B song of the Northern Parula (*Parula americana*) was described from 120 males recorded throughout much of the species' range in North America. Most songs were structured with a series of complex syllables, followed by simple syllables, trill syllables, and a terminal simple syllable. Some birds sang songs that contained 2 phrases per song with syllables that varied in structure and number between individuals. Analysis of song variables revealed variation at the macrogeographic level with songs from western populations differing significantly from eastern populations in song duration, frequency, number of trill syllables, and simple syllables. In addition, variation was evident between eastern and western populations in the structuring of phrase patterns. *Received 8 March 1999, accepted 3 August 1999.*

Several investigations into wood-warbler (Parulidae) song behavior have shown that some species sing two song types (Ficken and Ficken 1967, Morse 1967, Highsmith 1989) while other species have a repertoire of several songs classified as first and second category songs (Lein 1978, Staicer 1989, Byers 1995). The two song types have been referred to as types A and B (Morse 1967, Nolan 1978), types I and II (Lanyon and Gill 1964, Gill and Murray 1972, Morrisson and Hardy 1983), or accented and unaccented ending songs (Morse 1966, Lein 1978). Studies on the function of song suggest that type A, I, or accented ending songs [or the type B in Black-throated Green Warblers (*Dendroica virens*) and Blackburnian Warblers (*D. fusca*)] are used as intersexual signals and are more stereotyped; while B, II, or unaccented ending songs (or the type A in Black-throated Green and Blackburnian warblers) are used intrasexually and tend to be more variable (e.g., Kroodsma 1981, reviewed by Spector 1992).

Although detailed descriptions of parulid song types can be found for several species, a few, like the Northern Parula (*Parula americana*), are less well studied. Moldenhauer (1992) presented a detailed account of the type A song, but the type B song has yet to be described in detail spectrographically. In this study, I present a description of B songs recorded from several males located throughout the species' breeding range (eastern United States and southeastern Canada).

METHODS

Type B songs of 29 male Parula Warblers were recorded from 20 localities in Texas, Alabama, Mississippi, Louisiana, Georgia, and Tennessee (Appendix) from 15 May to 10 June 1986, during the morning hours of 07:00–10:00 (CST). Although no birds were color marked, only 1–3 individuals were recorded per locality, with two investigators recording different individuals, often at the same time. Type B songs were, in most instances, elicited by song playback. These recordings (46 songs) were made using a Uher 4000 Report IC recorder at a tape speed of 19 cm/sec and a Dan Gibson P650 parabolic microphone. Spectrograms of recorded songs were produced with a Kay Elemetrics 6061B sonagraph with a wideband filter. Additional song recordings were obtained from the Texas Bird Sound Library (Department of Biological Sciences, Sam Houston State University; 33 birds, 50 songs), Cornell Library of Natural Sounds (15 birds, 27 songs), and the Borror Laboratory of Bioacoustics of The Ohio State University (43 birds, 58 songs). These songs were recorded using Nagra III (38 cm/sec) or Magnemite (38 cm/sec) recorders. An AKG microphone (or an unknown type) was used with a parabola to record.

The following variables were measured for each song: (1) duration of song (sec), (2) total number of syllables, (3) number of syllable types, (4) minimum frequency, and (5) maximum frequency. For individuals with multiple recordings, I computed a within-bird mean. For the sake of comparison with variation as reported in the type A song (Moldenhauer 1992), I used analysis of variance (ANOVA; SAS Institute 1985; $\alpha = 0.05$) to test for significant differences between song populations from three geographic areas. Moldenhauer (1992) primarily reported on the differences between songs in the western versus eastern regions of the species' breeding range. I followed this

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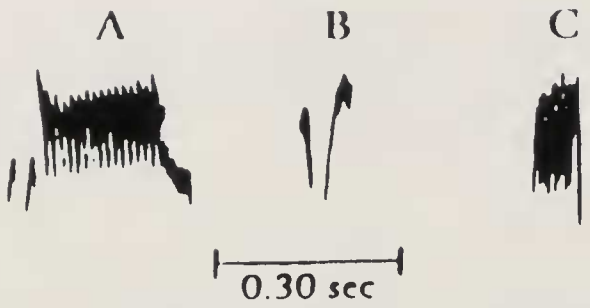

FIG. 1. Syllable classes of Northern Parula type B songs. (A) complex syllable (B) simple syllable (C) trill syllable.

division with the exception that I divide the eastern population into northeast and southeast (see Appendix). These geographical ranges correspond to the subspecies (western race, *P. a. ludoviciana*; southeastern race, *P. a. americana*; northeastern race, *P. a. pusilla*) proposed by Oberholser (1974).

I classified song elements based on morphological structure (Baptista 1974, Weins 1982, Bradley and Bradley 1983) using terminology partly adopted from Baptista (1974) and Staicer (1989). A note was any short tracing on the spectrogram, and syllables were represented by repeated notes or series of notes forming a coherent unit. Three classes of syllables were identified: (1) simple syllables (SS), those containing 1 or 2 simple notes; (2) complex syllables (CS), syllables with more than 2 notes forming a coherent unit, or in rare instances 1–2 wavy and continuous notes; (3) trill syllables (TS), high frequency slurs near the end of a song (Fig. 1). To distinguish between the number of different variations or types within each syllable class, a subscript number was added to a syllable's abbreviation (e.g., CS_{14}).

A phrase was defined as a series of repeated syllables forming the following 4 phrase classes of a B song: (1) complex (C) phrase, composed of complex syllables of one type; (2) mixed (M) phrase, composed of a mixture of repeated complex and simple syllables of one type each; (3) trill (T) phrase, composed of trill syllables of one type; (4) repeated trill (R) phrase, composed of trill syllables of 2 types (Fig. 2). A phrase pattern was the entire sequence of phrases in a song and was symbolized by the letter codes for each phrase class (e.g., C-T-SS = a song composed of a C phrase, T phrase, and ending with a simple syllable; Fig. 3).

RESULTS

Song structure.—Thirty-nine syllable types from 3 syllable classes were discovered in the type B song, including 21 complex syllables (Fig. 4), 11 simple syllables, and 7 trill syllables (Fig. 5). It appeared that no one individual contained more than one complex syllable type and no more than 2 types of simple and trill syllables.

Each of the syllable classes (complex, simple, and trill) was used to construct song phrases that typically began with an introductory series of complex syllables ($\bar{x}$ = 3.6 syllables per song, SD = 1.4, n = 181 songs) followed by a high frequency trill (T phrase) ($\bar{x}$ = 4.6 syllables per song, SD = 2.7, n = 181 songs) and ending in one to several simple syllables (SS; $\bar{x}$ = 0.88 syllables per song, SD = 2.6, n = 181 songs). Some birds sang songs that lacked a few of these syllable classes (e.g., only the introductory complex syllables were present) and therefore were shorter and usually more difficult to hear (low amplitude; e.g., somewhat like muted songs; Morse 1967). The number of syllables within a song ranged from 2 to 19.5 ($\bar{x}$ = 10.7), while most (54%) were composed of 10 to 15 syllables. Few songs contained more than 15 syllables (12.6%). Some birds began their song with chip notes (see Morse 1967) but this was rarely recorded and was not considered in this analysis.

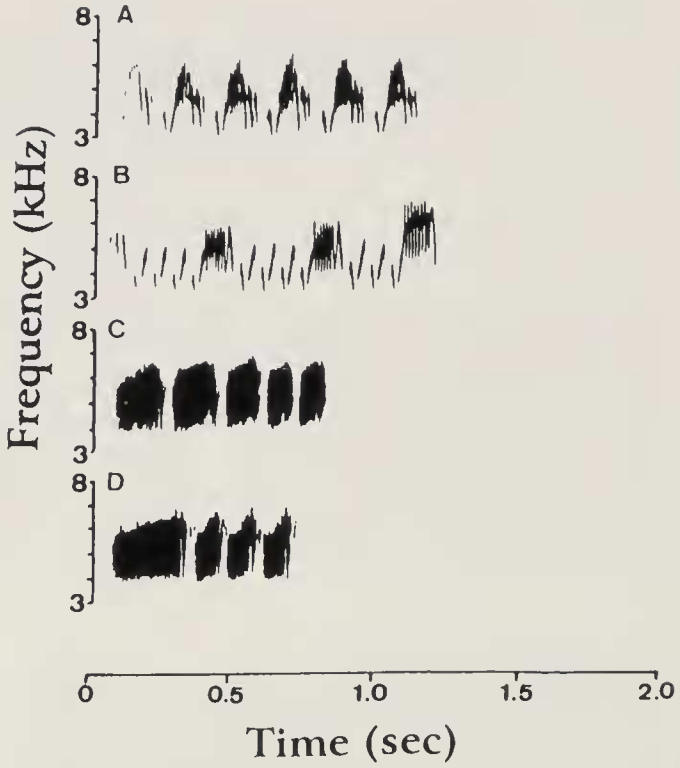

FIG. 2. Phrase classes of Northern Parula type B songs. (A) C phrase (B) M phrase (C) T phrase (D) R phrase.

The most frequent phrase pattern, C-T-SS (complex-trill-simple syllable), accounted for most of the songs (67%). Nine different patterns were found, the five most common are illustrated in Fig. 6. It is likely that some extremely rare patterns may represent scrambled

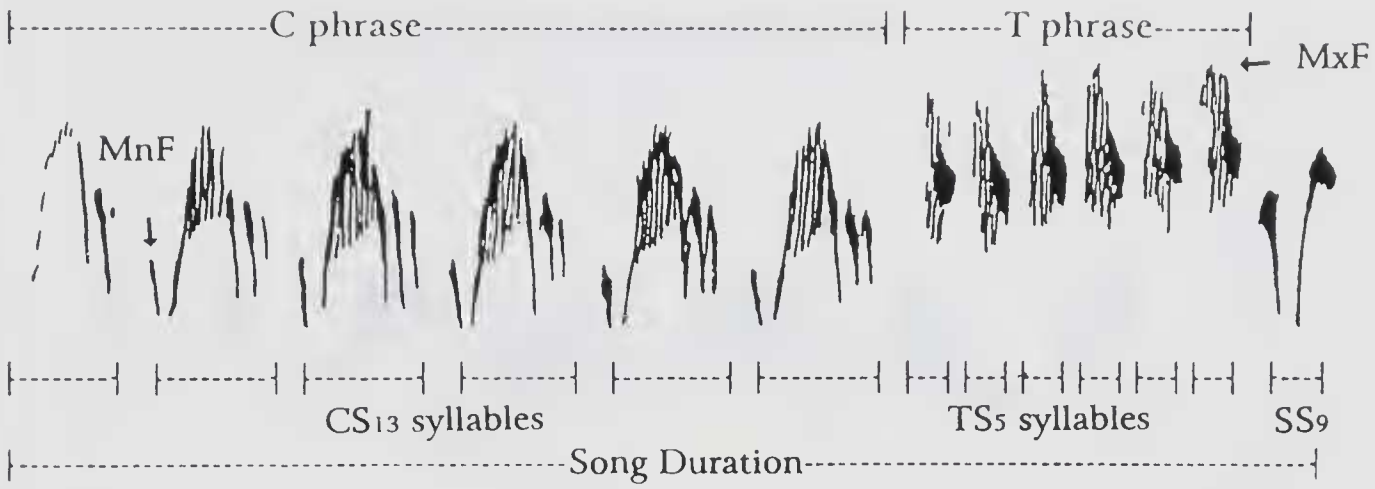

FIG. 3. Measurements and coding of a type B song. MxF = maximum frequency, MnF = minimum frequency, CS = complex syllable, TS = trill syllable, SS = simple syllable.

(e.g., T-M-T-SS occurred in 0.4% of songs) or incomplete song phrases (e.g., M occurred in 1.4% of songs and M-T occurred in 1.5% of songs).

Geographic variation.—Eight phrase patterns (except for the phrase C-T-SS) occurred in populations that occupied the western half of the species' breeding range and correspond to those birds that sang the western type A song (see Moldenhauer 1992). Birds occupying the eastern range and corresponding to those that sing the eastern type A song, sang B songs that were constructed of only three phrase patterns (C-T-SS, C-T, C; Fig. 6). The additional variation in phrase patterns observed for the western population is attributed to the addition of simple and complex syllables to the introductory portion of the song to form M phrases. This phrase difference appears to change or overlap between the Mississippi and Alabama boundary much as occurs with the type A song (Moldenhauer 1992). However, more data are needed to determine the distribution of type B song phrase patterns within the east to west type A song overlap zone.

In addition to phrase variation, songs varied significantly between geographic areas in mean duration, mean maximum frequency, and in the mean number of simple and trill syllables (Table 1). Songs of western birds averaged 0.10 second longer than songs of southeastern birds and 0.20 second longer than songs of northeastern birds ($F = 10.90$, df = 2, 134, $P < 0.001$). Birds from the latter region averaged 0.5 kHz less than the average maximum frequency of western and southeastern populations ($F = 4.31$, df = 2, 134, $P < 0.025$).

Comparing the usage of syllable types within the 3 syllable classes (complex, simple, and trill) among birds in the three geographic areas, the most frequent syllable for western birds was CS_{13} (56.6%; Fig. 4, no. 13) followed by T_2 (43.9%; Fig. 5, no. 8) and SS_8 (29.2%; Fig. 5, no. 8). For birds in the southeast, songs most frequently contained SS_8 (47.3%; Fig. 5, no. 8) followed by T_1 and T_2 (both at 39.4%; Fig. 5, no. 1 and 2, respectively). The most frequently used complex syllables for southeastern songs were CS_{13} (18.4%; Fig. 4, no. 13) and CS_4 (15.7%; Fig. 4, no. 4). Birds from the northeastern region primarily used T_3 (51.2%; Fig. 5, no. 3), CS_{19} (36.5%; Fig. 4, no. 19), and SS_9 (34.1%; Fig. 5, no. 9) to construct their songs. Of the three syllable types used to construct the type B song, significant differences were evident between the three geographical areas in the mean number of syllables used per song (Table 1). For instance, western singers used significantly more simple syllables to construct the type B song ($F = 16.3$, df = 2, 134, $P < 0.005$) but fewer trill syllables in comparison to eastern singers ($F = 23.9$, df = 2, 134, $P < 0.005$).

Only within specific localities did some birds sing identical songs (i.e., same phrase patterns and/or syllables), while others sang songs using a different type of one or more syllables within the three syllable classes (e.g., one individual might use CS_{13} and T_6, while

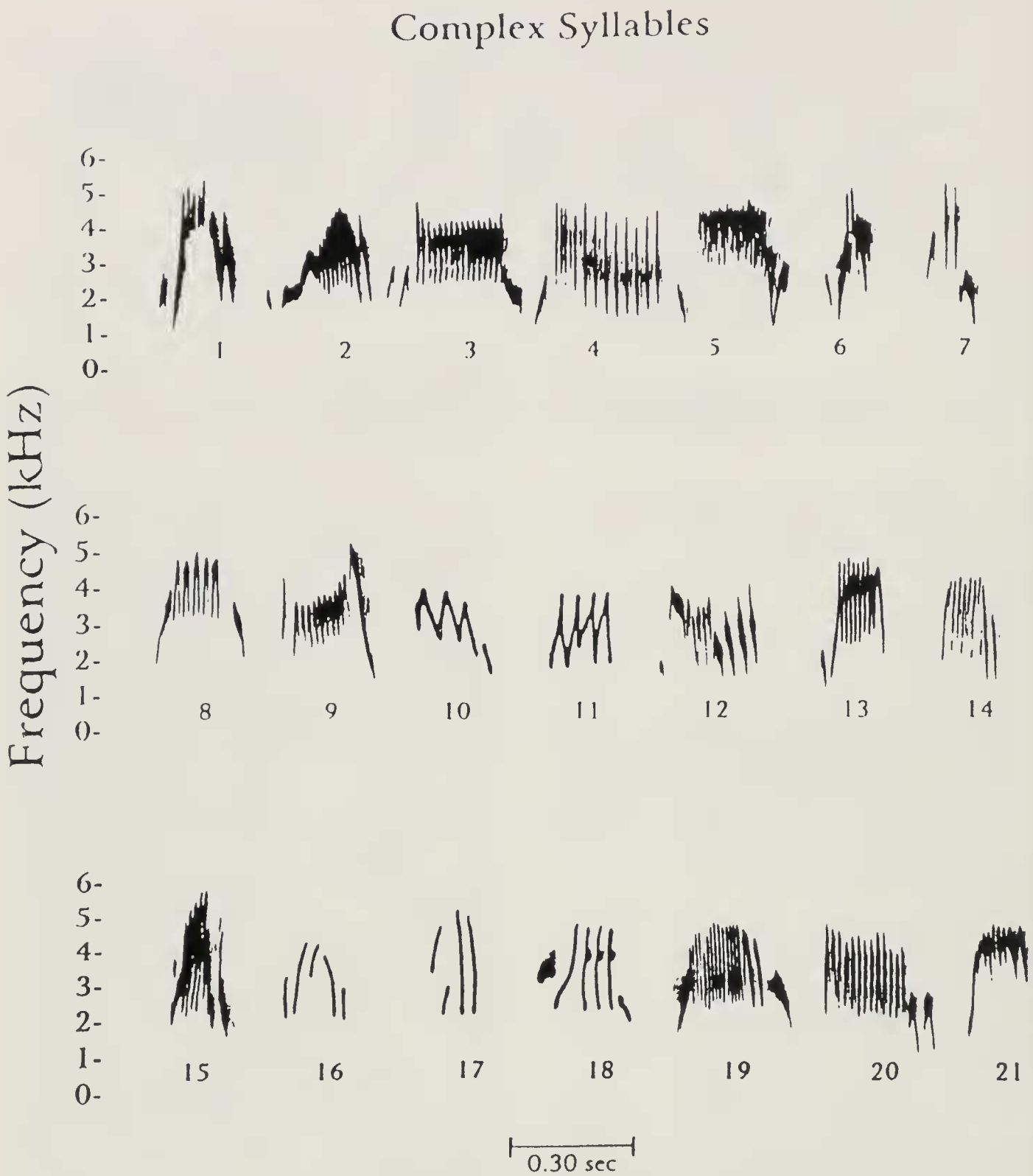

FIG. 4. Complex syllables of Northern Parula type B songs. Syllable types 1, 3, 5, 10, 11, and 20 from eastern birds only, while variants 14, 16, 17, and 18 from western birds only.

another used CS_4 and TS_7). It is unknown whether individuals with the same song (i.e., same phrase and syllables) within a specific locality were neighbors because most of these songs were not recorded by the author. It is likely that some of these individuals were members of the same local population because many of these songs were recorded within the same year. Some morphological differences were evident in specific syllable types between individuals (e.g., CS_{13} might differ slightly between two birds; Fig. 7). Morphological differences in simple syllables were evident between those used in the middle of

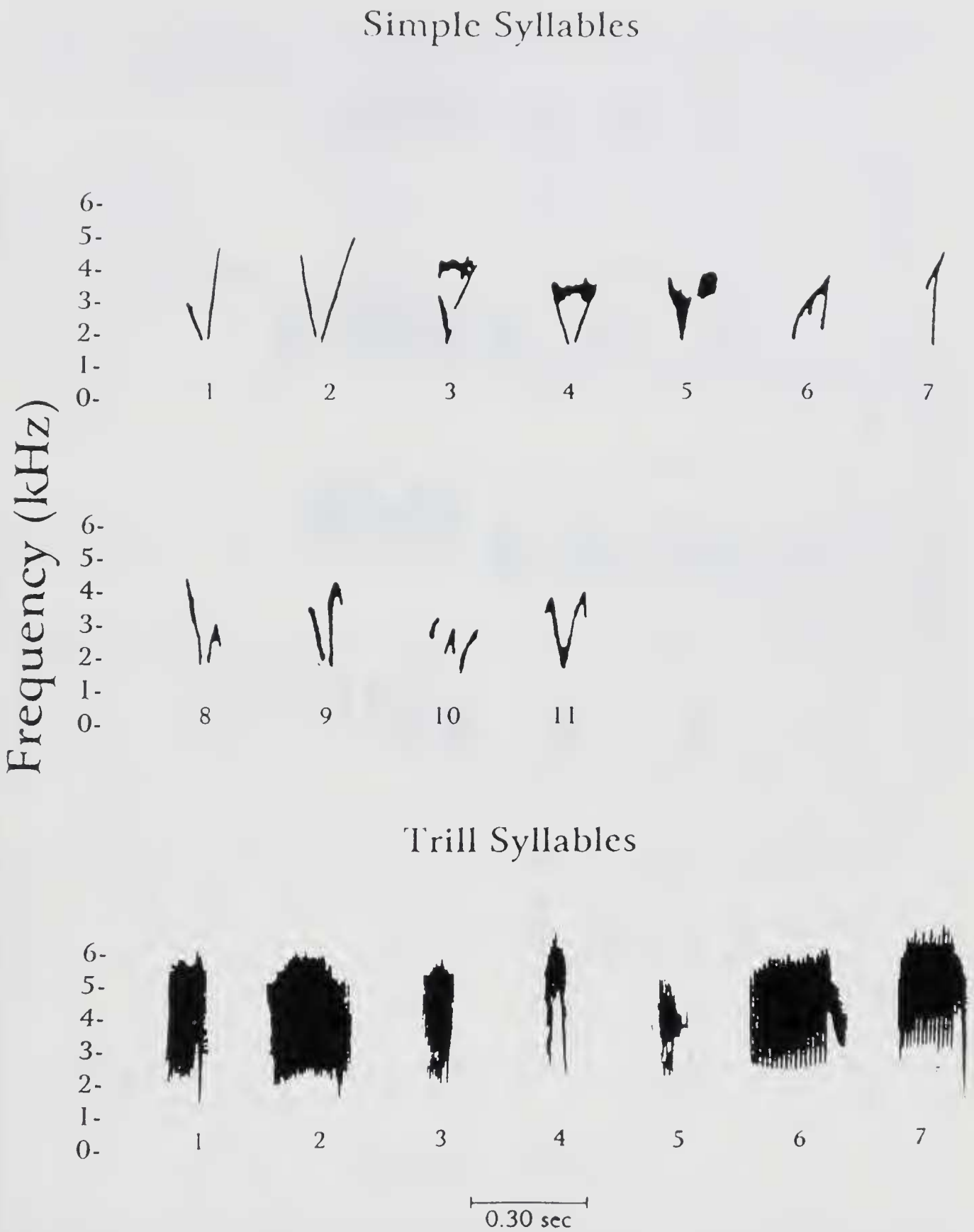

FIG. 5. Simple and trill syllables of Northern Parula type B songs. Simple syllable types 1, 3, and 5 and trill syllable type 6 from western birds only.

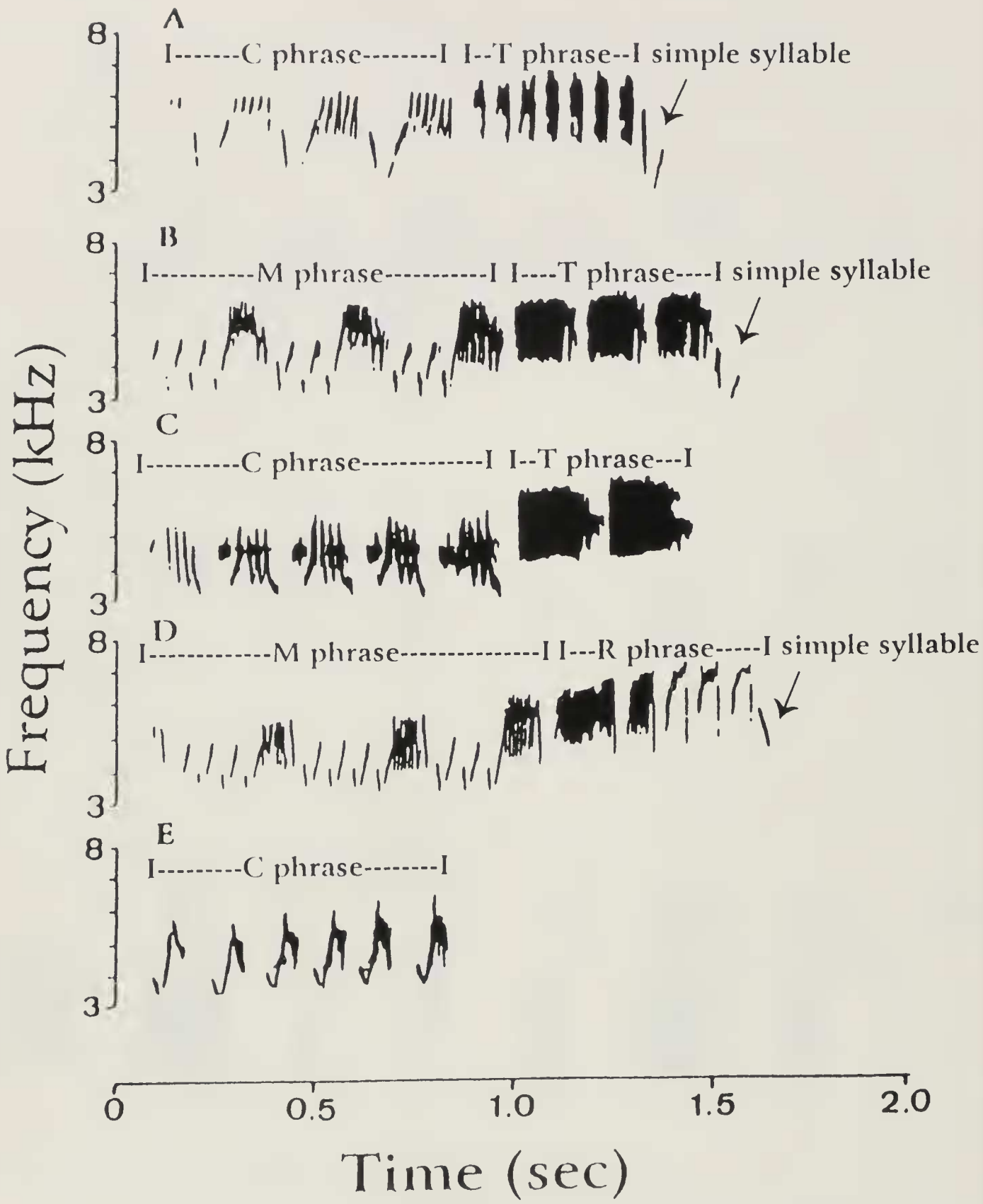

FIG. 6. The five most common song or phrase patterns observed in Northern Parula type B songs. (A) pattern C-T-SS [67% of all songs (west = 0.0%, southeast = 92%, northeast = 100%)], (B) pattern M-T-SS [13.1% of all songs (west = 45.0%, southeast = 0.0%, northeast = 0.0%)], (C) pattern C-T [6.2% of all songs (west = 17%, southeast = 2.6%, northeast = 0.0%)], (D) pattern M-R-SS [3.6% of all songs (west = 12.1%, southeast = 0.0%, northeast = 0.0%)], (E) pattern C [2.1% of all songs (west = 2.4%, southeast = 4.1%, northeast = 0.0%)].

TABLE 1. A comparison of song variables from western, southeastern, and northeastern type B songs of the Northern Parula (values are mean ± SD). Number of individuals in which songs were analyzed: West = 41, Southeast = 38, Northeast = 41.

Variable	Song population			ANOVA *F*-value[c]
	West	Southeast	Northeast	
Song duration (s)[a]	1.5 ± 0.2	1.4 ± 0.2	1.3 ± 0.1	10.90**
Number of syllables	11.9 ± 2.9	11.3 ± 3.1	11.4 ± 2.7	0.53
Syllable types in a song	4.0 ± 1.3	3.7 ± 1.0	3.6 ± 0.5	1.26
Maximum frequency (kHz)[a]	7.0 ± 0.4	7.2 ± 0.4	6.6 ± 0.4	4.31*
Minimum frequency (kHz)	4.4 ± 0.5	4.4 ± 0.5	4.2 ± 0.4	2.10
Complex syllables[a,b]	3.7 ± 1.6	3.5 ± 1.3	3.4 ± 0.9	0.71
Simple syllables[a,b]	4.6 ± 3.0	1.1 ± 1.0	1.0 ± 0.3	16.3***
Trill syllables[a,b]	2.9 ± 1.5	5.1 ± 2.6	6.5 ± 2.7	23.9***

[a] Multiple Comparison (Bonferroni Correction; $\alpha = 0.05$): Song Duration (W ≠ Se = Ne), Maximum Frequency (W = Se ≠ Ne), Simple Syllables (W ≠ Se = Ne), Trill Syllables (W ≠ Se ≠ Ne).
[b] Number per song.
[c] * $P < 0.025$, ** $P < 0.001$, *** $P < 0.0005$.

the song (to form M phrases) versus the single simple syllable terminating the song (as usually occurs in most parula B songs).

DISCUSSION

Song structure.—Northern Parula B songs are complex and show much intraspecific variation. Song complexity occurs because most songs contain multiple phrases (usually two) that vary in syllable types between individuals. A similar arrangement occurs in B songs of the Grace's Warbler (*Dendroica graciae*; Staicer 1989) and the type II song of the Blue and Golden-winged warblers (Gill and Murray 1972, Highsmith 1989). Some evidence suggests that complexity in B songs may be a result of intrasexual usage (e.g., territorial clashes between males), while A songs, used for mate attraction, are more stereotyped (Kroodsma 1981).

Geographic variation.—Northern Parula type A songs are very similar in most variables (except trill rate, frequency, and song length), but differ significantly between eastern and western populations in the type of terminal syllable (Moldenhauer 1992). Males from each population recognize and respond differentially to the two types of A songs (Regelski and Moldenhauer 1996). Similarly, the type B song exhibited differences between eastern and western populations in song length and maximum frequency, but primarily differed in the number of specific syllable types and phrase patterns composing songs. For instance, western birds frequently used more simple syllables per song and often used these syllables to construct the M phrase pattern, which was absent from eastern singers.

Moldenhauer (1992) argued for subspecific recognition of *P. americana* (*P. a. americana* for the east and *P. a. ludoviciana* for the west) based upon the terminal note difference in the type A songs. Results from my study are consistent with this division, based upon B song phrase patterning between eastern and western populations. The terminal note in the type A song is readily identifiable both audibly and visually by sonogram. Likewise, B songs with M phrases (western population) may be audibly distinguished from songs without M phrases (eastern population); they are longer (composed of more syllables) and more buzzy. These differences are easily viewed by comparing sonograms (Fig. 6B, D vs Fig. 6A, C). Whether these structural differences in eastern and western type A and B songs are influenced by learning and/or have a genetic basis has yet to be determined.

Populations from each geographic region contained a repertoire of unshared syllables (15.3% confined to the eastern population, 20.5% confined to the western population); however, many (57%) were shared. Syllable confinement within specific macrogeographical areas reported in my study might be viewed with some speculation. For instance, some individual songs contained more than one syllable type within a syllable class, particularly trill and simple syllables. No individ-

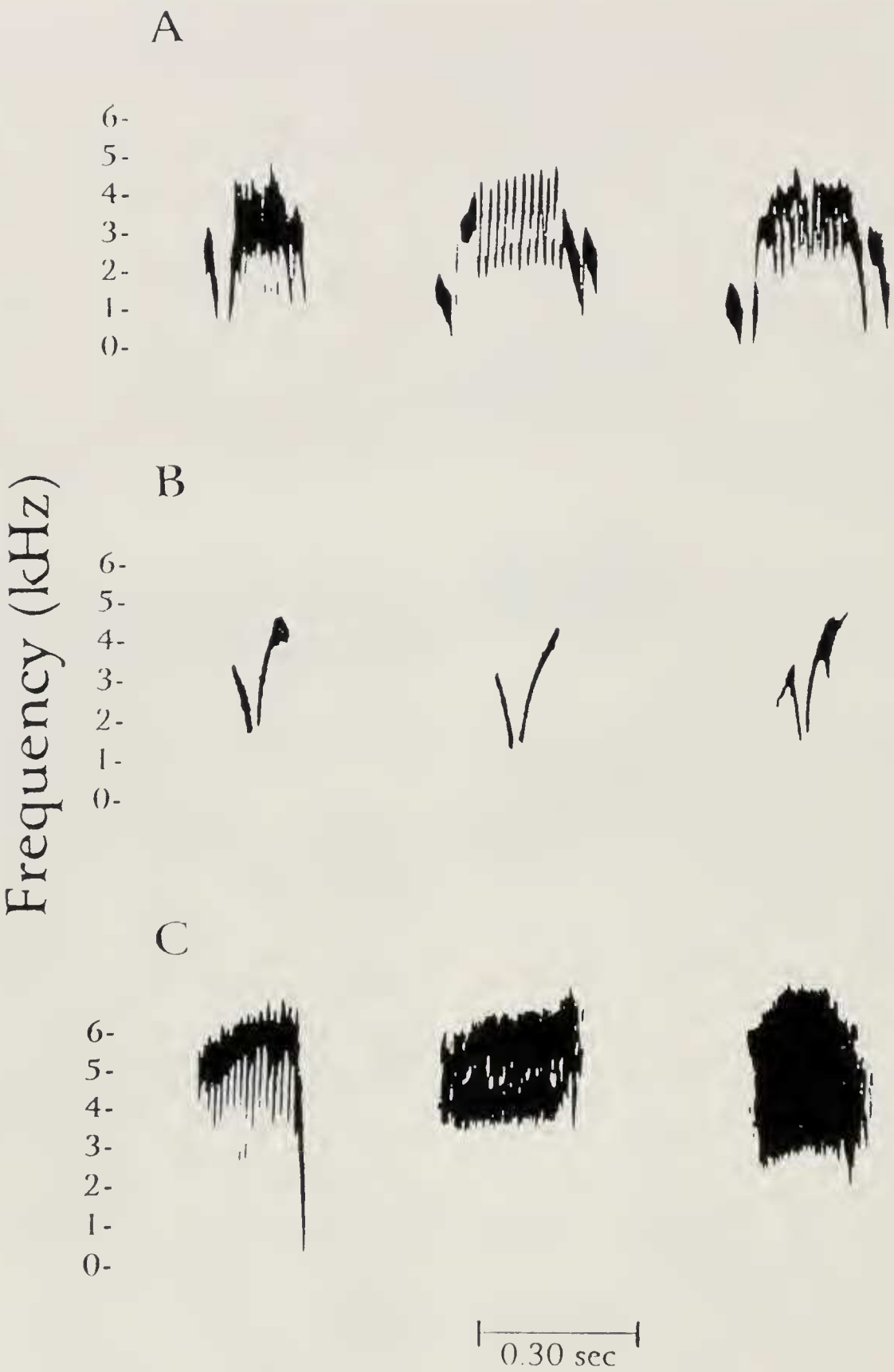

FIG. 7. Examples of morphological variations of specific syllable types between individuals (A) CS_{13} (complex syllable), (B) SS_1 (simple syllable), (C)TS_2 (trill syllable).

uals for which multiple songs were examined sang more than 1 complex syllable type. However, because of the small sample size (only 5 individuals recorded with at least 5 songs from each), these results should be viewed with caution. Within specific microgeographic areas, syllable sharing could be variable even though a few individuals sang some or all of the same syllables.

In other warbler species that have a song similar to the type B of the Northern Parula, local dialect patterns are usually evident, which suggests that young males learn B songs from neighboring conspecifics (Kroodsma 1981). Thus an individual from an area that contains a song similar to his neighbors, will be more effective during countersinging bouts (Kroodsma 1981). Playback experiments show that Blue-winged Warbler males respond more intensely to their local type II (B) songs but do not differentiate among type I (A) songs of different localities (Kroodsma et al. 1984). Although Northern Parula B songs tend to be complex and differ between locations (in either phrase pattern or syllable types used), Bay (1987) found no discernable patterns or dialects in songs from the two best sampled areas (representing 10 and 15 individuals) in Texas.

Future studies should concentrate on gathering information concerning site fidelity in successive breeding years to allow a better understanding of type B song structure at the microgeographic level. Such data might also reveal whether young males learn the same types of syllables and phrase patterns in successive years or different ones as a result of the exposure to new individuals. In addition, researchers should determine what role, if any, the disjunct winter distribution of the Northern Parula has on song learning and the geographical differences in the type A and B songs on the breeding grounds

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APPENDIX

Recording localities for Northern Parula type B songs. Localities are listed by geographic region and then alphabetically by state (or country) and county, parish, or province. Number of individuals per locale are indicated in parenthesis.

Southeast region.—Alabama: Dale (1), Dallas (1), Clark (1), Covington (2), Monroe (2), Wilcox (4). Florida: Alatchua (1), Dade (3), Flager (1), Jefferson (2), Polk (1), Wakulla (1). Georgia: Bulloch (3), Chatham (4), Jenkins (6), Richmond (1). North Carolina: New Hanover (3). South Carolina: Richland (8). Tennessee: Dickson (1), Sevier (1).

Northeast region.—Canada: Gaspe (1). Maine: Lincoln (44). Ohio: Franklin (2), Seneca (1). West Virginia: Monogalia (1).

West region.—Lousiana: St. Tammany (2). Mississippi: George (3), Hancock (4). Texas: Hardin (2), Montgomery (2), Trinity (2), Walker (25).